Landscape-level influences of terrestrial snake occupancy within the southeastern United States

David A. Steen,[1,2,10] Christopher J. W. McClure,[2] Jean C. Brock,[1] D. Craig Rudolph,[3] Josh B. Pierce,[3] James R. Lee,[4] W. Jeffrey Humphries,[5] Beau B. Gregory,[6] William B. Sutton,[7] Lora L. Smith,[1] Danna L. Baxley,[8] Dirk J. Stevenson,[9] and Craig Guyer[2]

[1]*Joseph W. Jones Ecological Research Center, 3988 Jones Center Drive, Newton, Georgia 39870 USA*
[2]*Department of Biological Sciences, Auburn University, Auburn, Alabama 36849 USA*
[3]*U.S. Forest Service Southern Research Station, Nacogdoches, Texas 75965 USA*
[4]*The Nature Conservancy, CSJFTC-ENV Building 622, Camp Shelby, Mississippi 39407 USA*
[5]*North Carolina Wildlife Resources Commission, Chapel Hill, North Carolina 27516 USA*
[6]*Coastal and Nongame Resources Division, Louisiana Department of Wildlife and Fisheries, Baton Rouge, Louisiana 70808 USA*
[7]*Department of Forestry, Wildlife, and Fisheries, University of Tennessee, Knoxville, Tennessee 37996 USA*
[8]*Kentucky Department of Fish and Wildlife Resources, Frankfort, Kentucky 40601 USA*
[9]*The Orianne Society, Indigo Snake Initiative, Clayton, Georgia 30525 USA*

Abstract. Habitat loss and degradation are thought to be the primary drivers of species extirpations, but for many species we have little information regarding specific habitats that influence occupancy. Snakes are of conservation concern throughout North America, but effective management and conservation are hindered by a lack of basic natural history information and the small number of large-scale studies designed to assess general population trends. To address this information gap, we compiled detection/nondetection data for 13 large terrestrial species from 449 traps located across the southeastern United States, and we characterized the land cover surrounding each trap at multiple spatial scales (250-, 500-, and 1000-m buffers). We used occupancy modeling, while accounting for heterogeneity in detection probability, to identify habitat variables that were influential in determining the presence of a particular species. We evaluated 12 competing models for each species, representing various hypotheses pertaining to important habitat features for terrestrial snakes. Overall, considerable interspecific variation existed in important habitat variables and relevant spatial scales. For example, kingsnakes (*Lampropeltis getula*) were negatively associated with evergreen forests, whereas Louisiana pinesnake (*Pituophis ruthveni*) occupancy increased with increasing coverage of this forest type. Some species were positively associated with grassland and scrub/shrub (e.g., Slowinski's cornsnake, *Elaphe slowinskii*) whereas others, (e.g., copperhead, *Agkistrodon contortrix*, and eastern diamond-backed rattlesnake, *Crotalus adamanteus*) were positively associated with forested habitats. Although the species that we studied may persist in varied landscapes other than those we identified as important, our data were collected in relatively undeveloped areas. Thus, our findings may be relevant when generating conservation plans or restoration goals. Maintaining or restoring landscapes that are most consistent with the ancestral habitat preferences of terrestrial snake assemblages will require a diverse habitat matrix over large spatial scales.

Key words: Agkistrodon contortrix; Coluber spp.; Crotalus spp.; detection probability; Elaphe spp.; Heterodon platirhinos; Lampropeltis getula; landscape ecology; occupancy modeling; Pituophis spp.; squamate reptile; Thamnophis sirtalis.

Introduction

Habitat loss, degradation, and fragmentation are thought to be primary drivers of species extirpations and extinctions (Wilcove et al. 1998). However, for many species we have little idea how or why habitat change influences their populations (Gardner et al. 2007). Reptiles in particular are an imperiled group of organisms (Gibbons et al. 2000), and many snake species are of conservation concern (Mullin and Seigel 2009). This imperilment (and associated population declines) has been suggested to have important and negative implications for the ecosystems in which snakes play significant roles (Reading et al. 2010), yet for many species we lack basic natural history information vital to formulating advanced study questions or generating conservation plans (Dodd 1987, Greene 2005). The most relevant information may be what constitutes suitable habitat for a species (Johnson 1980).

Habitat selection for a given species is often quantified by examining habitat use of animals within an occupied

area. Selection at this spatial scale allows us to determine what habitats individual animals use while they are in a given site, but not the ultimate factors influencing why a species is present at a site. Because habitat selection may occur on a spatial scale larger than the home range (e.g., Moore and Gillingham 2006, Lagory et al. 2009, Steen et al. 2010a, Baxley et al. 2011), it is important to consider habitat requirements on large and multiple scales. Intrinsic habitat features of a given occupied site may have less to do with occupancy than landscape-level habitat features (Buler et al. 2007).

Our knowledge of habitat selection in vertebrates is typically based on comparisons of use vs. availability (i.e., compositional analysis; Johnson 1980, Aebischer et al. 1993). Relevant data are often collected via intensive radiotelemetry studies of a relatively small number of individuals within discrete populations, with each location treated as an independent data point (e.g., Gerald et al. 2006, Halstead et al. 2009, Lagory et al. 2009). Euclidean distance methods also have been used to identify habitat selection in vertebrates (e.g., Steen et al. 2010a, Baxley et al. 2011). These methods are based on comparisons of mean distances from individuals to particular habitat types and mean distances from random points to the different habitat types (Conner and Plowman 2001). When individual animals use a particular habitat in greater proportion than its availability would suggest (in the case of compositional analysis), or are located closer than random points to a particular habitat type (in the case of distance-based analysis), this habitat may be interpreted as being important for the species. These methods have been instrumental in formulating our understanding of habitat selection of individual animals; however, most radiotelemetry studies have been focused on a relatively small scale, both in terms of the number of monitored individuals and the spatial extent of the area they inhabit.

Another method of quantifying habitat preference or suitability has been to acquire raw counts or abundances of animals captured via passive trapping and inferring preference by comparing relative numbers (e.g., Ford et al. 1991, Cagle 2008, Todd and Andrews 2008). However, abundance may be a poor proxy for vital rates (e.g., survivorship; Todd and Rothermel 2006) and variation in detection probability may limit straightforward interpretation of abundance data (Mazerolle et al. 2007). Analytical methods that incorporate detection probability may be appropriate for some aquatic and semi-aquatic snakes (Lind et al. 2005, Koons et al. 2009, Durso et al. 2011, Willson et al. 2011); their relatively high capture probabilities allow for greater flexibility in analysis than when studying terrestrial species, which may be infrequently detected or recaptured (Steen 2010, Steen et al. 2012).

There is an increasing body of knowledge regarding what habitats individual snakes may use at a particular site or which habitats contain greater numbers of animals, but limited research has been conducted to determine whether certain habitats within a site influence species occupancy. This species-level selection may be the ultimate criterion regarding evaluation of habitat suitability. Occupancy modeling offers a potential method of (1) examining habitat selection at the species level while (2) incorporating variation in detection probability (MacKenzie et al. 2002, Mazerolle et al. 2005, Luiselli 2006, Long et al. 2011). Therefore, to identify how landscape-level land cover influences the presence of snakes, we modeled occupancy probabilities for 13 species based on capture data from 449 traps located across the southeastern United States while evaluating 12 competing hypotheses potentially explaining occupancy patterns. To guide land managers, we also report species occupancy probabilities in relation to different levels of land cover categories; this information serves to identify habitat features that should be incorporated into restoration efforts intending to increase habitat suitability for a given species.

MATERIALS AND METHODS

Snake trap data

We focused our modeling efforts on 13 primarily terrestrial species native to the southeastern United States and relatively vulnerable to standard snake-trapping methodology (i.e., passive trapping via box and funnel traps together with drift fence arrays; Burgdorf et al. 2005), including the copperhead (*Agkistrodon contortrix*), North American racer (*Coluber constrictor*), coachwhip (*Coluber flagellum*), eastern diamond-backed rattlesnake (*Crotalus adamanteus*), timber rattlesnake (*Crotalus horridus*), red cornsnake (*Elaphe guttata*; cornsnakes east of the Mississippi River; Burbrink 2002), Slowinski's cornsnake, (*Elaphe slowinskii*; cornsnakes in western Louisiana and eastern Texas; Burbrink 2002), eastern hog-nosed snake (*Heterodon platirhinos*), pinesnake (*Pituophis melanoleucus*), Louisiana pinesnake (*Pituophis ruthveni*; Reichling 1995, Rodríguez-Robles and Jesús-Escobar 2000), and common gartersnake (*Thamnophis sirtalis*). Species identities are problematic for two additional snakes, the kingsnake and the ratsnake (Burbrink et al. 2000, Burbrink 2001, Pyron and Burbrink 2009b). Because precise geographic separation of these species has not been described, they may interbreed where they co-occur, and habitat use is likely to be similar for all forms, we pooled all ratsnakes (hereafter *Elaphe obsoleta*; i.e., *E. alleghaniensis*, *E. spiloides*, and *E. obsoleta* of Burbrink [2001]) and, separately, we pooled all kingsnakes (hereafter *Lampropeltis getula*; i.e., *L. getula*, *L. nigra*, and *L. holbrooki* of Pyron and Burbrink [2009a]).

We used data from a variety of multiyear upland snake-trapping efforts within the southeastern United States. All data were collected via passive trapping, specifically drift fences in association with box traps or funnel traps designed to capture large upland snakes (Burgdorf et al. 2005). We condensed captures within an

annual activity season such that for each trap, a species received a "1" if it was detected in a given year and a "0" if it was not. Therefore, the number of surveys for each site was equivalent to the number of years it was monitored. Considerable effort may be required to determine whether a species is present (or absent) at a site (Kéry 2002); by examining our data at a relatively long temporal scale (i.e., equating an annual active season of trapping as one sampling occasion), we increased our probability of detection. Similarly, short-term weather patterns may influence detection; trapping effort varied, but generally included multiple months of active-season trapping in any particular year (i.e., the months of the year that are warm enough to facilitate snake movement). Therefore, we assume that the large temporal scale of our data reduces the impact of short-term changes in detection probability due to environmental conditions. Traps were monitored for differing periods of time: 2–7 years (Table 1).

Multiple traps were located in close proximity (200 m apart) and were distributed along transects within similar and continuous habitat at seven sites in Texas and Louisiana (Rudolph et al. 2006); six sites contained five traps and one contained four traps. Trap data were condensed within each of these sites and hereafter are treated as single traps. Although condensing these trap data may have influenced our estimated detection probability at these sites, we suggest that it did not substantially alter our results related to occupancy, because traps within a site were located within comparable habitat. We lacked data from central Florida southward, an area that contains endemic habitats (e.g., Florida scrub) and may experience unique trends influencing species composition (e.g., Means and Simberloff 1987). We suggest that the trends we identified are applicable, at least for the area between our trap locations (Fig. 1).

Land cover data

We used 2001 National Land Cover Data (NLCD, 30-m pixels; Homer et al. 2004) to characterize habitat around each trap. We condensed several land cover categories that we considered likely to be structurally similar (Table 2), because habitat structure may be more important to snakes than dominant plant species (Reinert 2001, Vitt 2001). We used ArcGIS version 9.3.1 (ESRI 2009) to determine the area of each land cover category within multiple spatial scales (250-, 500-, and 1000-m radius buffers) to avoid an a priori identification of an appropriate scale (Jenkins et al. 2009). Buffer sizes were arbitrarily chosen. Visual inspection of the land cover category "Developed" revealed that the vast majority of this cover class within our buffers represented roads due to the rural locations of trap arrays.

We were unable to determine accurate coordinates for 15 traps (one project) and therefore could not characterize surrounding land cover for these. In addition, the forest surrounding other traps (<25) had experienced forest management (e.g., selective thinning) influencing the total coverage of pertinent land cover classes between the time the NLCD were collected and when snake traps were deployed; we removed measurements for any habitat that experienced significant human-induced change. Because Program PRESENCE (Hines 2010) cannot incorporate missing covariate data, we used median values to replace all missing land cover data. Not all traps were within the geographic range of a given species. When we generated median values, we did so independently for each species and only spatial land cover data surrounding traps placed within the geographic range of that species were used (based on range maps in Ernst and Ernst [2003]). All covariates that were continuous variables were z-transformed.

Occupancy modeling

We outlined our objectives (i.e., to identify habitat features that may influence snake occupancy and the spatial scale that best predicted this parameter) before model development (Jenkins et al. 2009). We constructed 10 competing models representing various hypotheses pertaining to important influences on snake habitat use, as suggested in previous studies (Table 3). Because habitat heterogeneity may be an important consideration (e.g., Hoss et al. 2010), we included a model containing five habitat categorizations. We also grouped traps according to the project with which they were associated and included a model with only project as a covariate to determine whether there were project or site-specific idiosyncrasies unmeasured within this study that were important occupancy predictors. We also included a null model that held occupancy constant across all sites. We assumed that each site was closed to change in occupancy status (i.e., no species colonized a given area or was extirpated within that area over the course of the study).

We excluded funnel traps when building models for some large species (P. melanoleucus, C. adamanteus, and C. horridus) because this trap type is likely to be less effective than box traps at capturing these animals; no funnel traps were used within the range of P. ruthveni. Trap arrays were generally >100 m apart, so we treated them as independent sites. Although it is possible for an individual snake to visit multiple traps (e.g., Steen et al. 2007a), we consider this an unusual event. Similarly, because the distance between traps was sometimes less than our buffer sizes, there was occasionally some buffer overlap. The overlap of buffers, which occurred largely within a project rather than between them, raises the potential of spatial autocorrelation, but we did not consider this to be an important consideration if occupancy models with project as a covariate fared relatively poorly. To ensure that patterns were due to landscape-scale habitat features, rather than geographic limits to a particular species' distribution, we only

TABLE 1. Projects generating snake detection/nondetection data used to model occupancy across the southeastern United States.

Location	State	Total traps	Trap type	Years monitored	Source
Fort Stewart Military Reservation	Georgia	6	funnel	1999–2000	Stevenson et al. (2003)
Charleston, Dorchester, Hampton, and Jasper Counties	South Carolina	27	box	2001–2003	Humphries (2005)
Conecuh National Forest	Alabama	12	box	2005–2006	Guyer et al. (2007)
DeSoto National Forest (and surrounding areas)	Mississippi	5	funnel	2004–2006	Baxley and Qualls (2009)
Camp Shelby Joint Forces Training Center	Mississippi	34	box	2005–2009†	Lee (2009)
Joseph W. Jones Ecological Research Center (Ichauway)	Georgia	16	box	2005–2008	Linehan et al. (2010)
William B. Bankhead National Forest	Alabama	18	box	2006–2009‡	Sutton et al. (2010)
Solon Dixon Forestry Education Center	Georgia	15	box	2002–2004	Steen et al. (2010b)
Eglin Air Force Base	Florida	19	box	2009–2010	Steen et al., *unpublished data*
Eastern Texas and western Louisiana (various)		299	box	1992–2009§	Rudolph et al. (2006)
Western Louisiana, private industrial timberlands		25	box	2007–2009¶	

† During this time period, 16 traps were monitored for two years, and 18 traps were monitored for three years.
‡ Individual traps were monitored for a total of three years each during this four-year period.
§ Individual traps were monitored from varying periods of time (2–7 years).
¶ Rudolph et al. (2006) can be consulted for comparable methodology.

included projects within the geographic range of a particular species when building detection probability or occupancy models for that species.

We considered detection probability to be a nuisance parameter; therefore we first modeled detection probability, using the single-season model (MacKenzie et al. 2002) in Program PRESENCE (Hines 2010) for each species as (1) constant, (2) varying by year, or (3) varying by project. We used the best predictor of detection probability, ranked by Akaike's Information Criterion, AIC (Burnham and Anderson 2002) for each species in successive occupancy models. Due to low numbers of detections and to reduce the number of parameters in our models, we assumed a constant
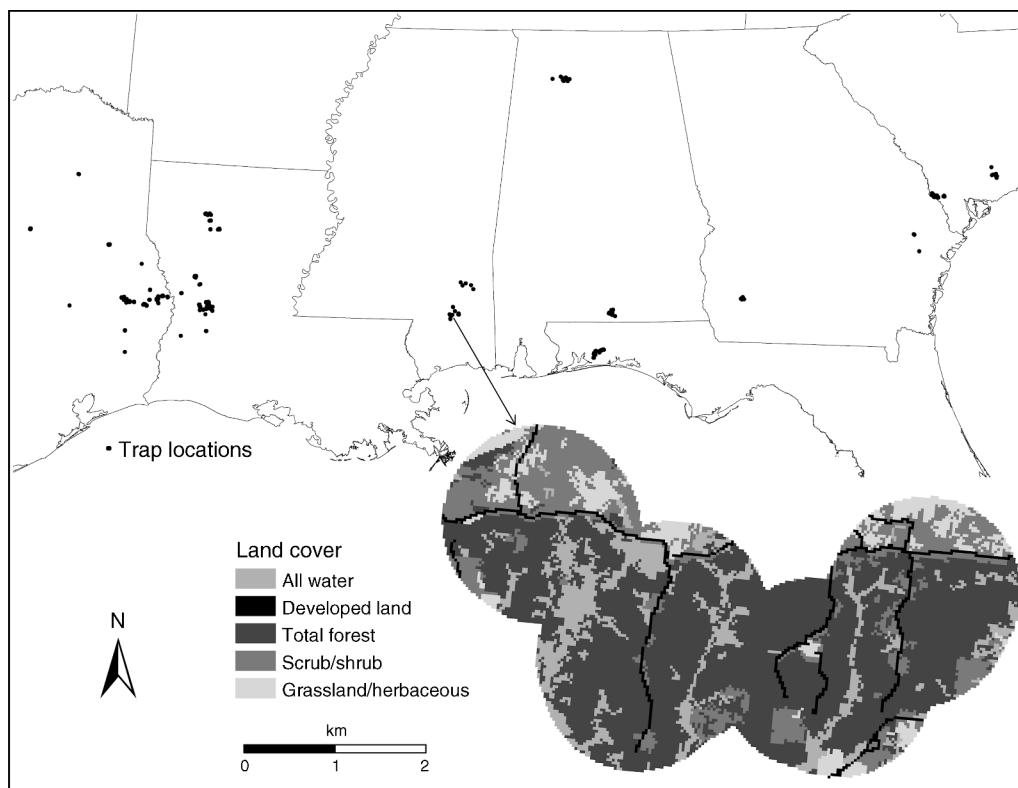

FIG. 1. Locations of traps throughout the southeastern United States used in modeling occupancy of 13 large terrestrial snake species. The inset of land cover types contains only a representative subset of land cover categories used when constructing models (Table 1). Not pictured are traps associated with the Solon Dixon Forestry Education Center, which were adjacent to traps located within Conecuh National Forest in south-central Alabama.

TABLE 2. National Land Cover Data categorizations used within the current study.

Land cover variable	Land cover composition	Abbreviation
All water	open water woody wetlands emergent herbaceous wetland	Allwater
Developed land	developed, open space developed, low intensity developed, medium intensity developed, high intensity	Roads
Deciduous forest		Dec
Evergreen forest		Everg
Mixed forest		Mixed
Total forest	deciduous forest evergreen forest mixed forest	Forest
Scrub/shrub		Scrub/Shrub
Grassland/ herbaceous		Grass

detection probability for *P. ruthveni*, *C. horridus*, and *C. adamanteus*.

We also used the single-season model within Program PRESENCE to model occupancy. The 12 competing models were constructed three times each (once for each scale) for each species. We ranked models by AIC_c (AIC adjusted for small sample size; Burnham and Anderson 2002). For each iteration, we calculated the over-dispersion parameter ($\hat{c}$) using a global model (Burnham and Anderson 2002). We then used $\hat{c}$ to correct AIC_c for overdispersion ($QAIC_c$; Burnham and Anderson 2002) and reported model weight (w_i). Standard errors were also corrected by $\hat{c}$ (Burnham and Anderson 2002). We considered a model to be competitive for inference if $\Delta QAIC_c \leq 2.0$ (Burnham and Anderson 2002), and if the model did not contain uninformative parameters (Arnold 2010). Assuming that a parameter within a model with strong support was informative (Arnold 2010), we interpreted trends even if 95% confidence intervals included zero by noting that the parameter was included in the model(s) best explaining occupancy. When 95% confidence intervals did not include zero for a parameter that appeared in a top model, we reported a significant association between this parameter and occupancy probability. For Fig. 2, we reported only those parameters in which 95% confidence intervals did not include zero.

We used a sequential decision-making framework to refine model selection. For all species that we evaluated, detection probability was best estimated when allowed to vary by project. If a model garnering strong support was unable to reach convergence to more than three digits and produced faulty standard errors when producing detection probabilities at a particular site, we grouped that site into the intercept. In these cases, we standardized detection probability covariates for each

species on all three scales, to enable comparison. Top models were not used for inference if there were still problems constructing a variance/covariance matrix or if there were problems obtaining standard errors for occupancy estimates. For each species, we took competitive models from all three scales and used $QAIC_c$ to determine which scale best predicted snake occupancy. Again, models with $\Delta QAIC_c \leq 2.0$ were considered to receive strong support if they did not contain uninformative parameters (Burnham and Anderson 2002, Arnold 2010).

RESULTS AND DISCUSSION

For most of the species included within this study, it is likely that populations are able to persist in habitats other than those we identified as important. However, investigating habitat preference within a large-scale matrix of suitable habitat types allowed us to elucidate which are selected by the species when a variety of habitats is available. We report species-level occupancy probabilities for snakes significantly associated with specific land cover categories (Fig. 2), thereby identifying habitats that should be considered when generating management plans or determining habitat suitability. Positive relationships suggest that a particular habitat type is important for a given species, whereas negative relationships identify habitats that need not be emphasized.

We documented considerable interspecific variation in land cover types that were important predictors of snake occupancy. Although our data suggest that different species respond to habitat at different spatial scales, there was only one species (*C. horridus*) for which models from two different spatial scales garnered strong support (Table 4). This suggests that, for each species, occupancy was typically best predicted by the landscape at only one of the scales evaluated, even as evidence

TABLE 3. Combinations of covariates used to model occupancy probability (Ψ) and relevant citations forming the basis of various hypotheses.

Model	Source of hypotheses
$\Psi(Dec), p(x)$	Ford et al. (1991)
$\Psi(Everg), p(x)$	Waldron et al. (2006)
$\Psi(Forest), p(x)$	Steen et al. (2010a)
$\Psi(Scrub/Shrub), p(x)$	Halstead et al. (2009)
$\Psi(Forest+Grass), p(x)$	Blouin-Demers and Weatherhead (2001)
$\Psi(Forest+Allwater), p(x)$	Roe et al. (2003)
$\Psi(Scrub/Shrub+Grass), p(x)$	Lagory et al. (2009)
$\Psi(Dec+Everg+Mixed+ Scrub/Shrub+Grass), p(x)$	Hoss et al. (2010)
$\Psi(Dec+Allwater), p(x)$	Steen et al. (2007b)
$\Psi(.), p(x)$	this study
$\Psi(Project), p(x)$	this study
$\Psi(Roads), p(x)$	Rudolph and Burgdorf (1997)

Notes: All hypotheses were evaluated for each species included within this study. Abbreviations are provided in Table 1; p is detection probability, and x denotes the covariates used to model detection probability, which varied by species.
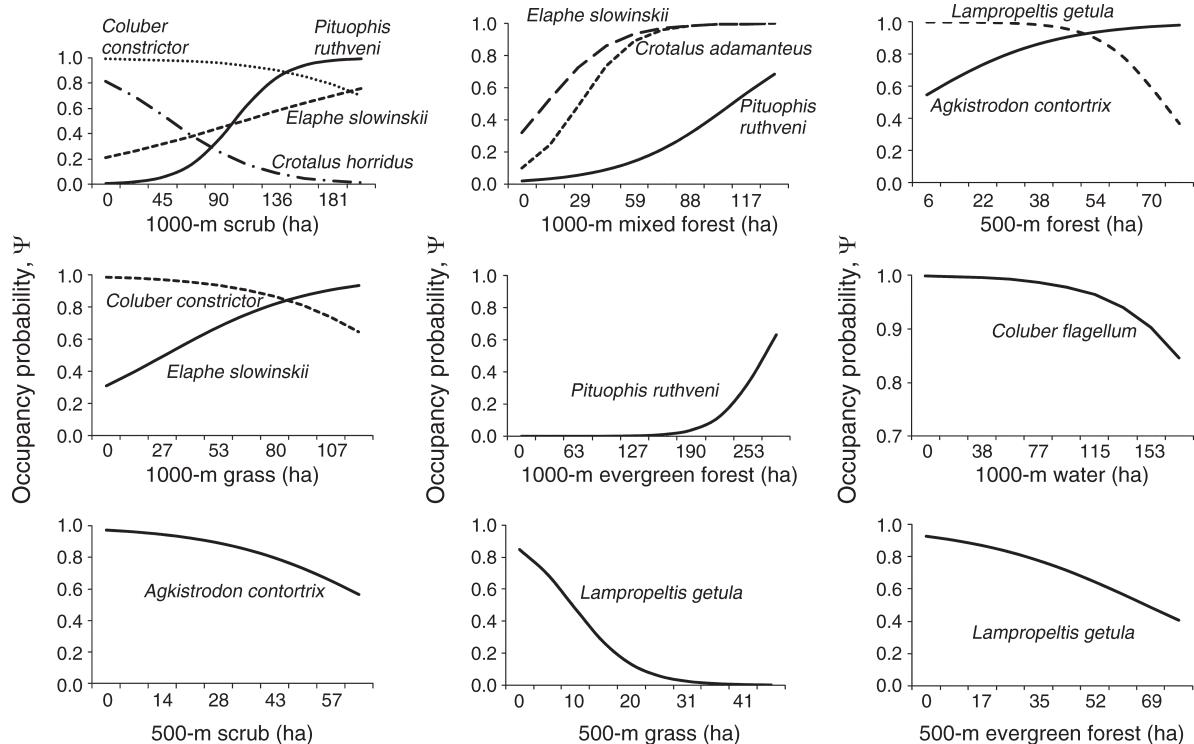
FIG. 2.   Relationships between landscape and habitat variables (x-axes) and occupancy probabilities (y-axes) of terrestrial snake species in the southeastern United States. Land cover types surrounding each trap are presented at different spatial scales (as 500- and 1000-m buffers). We only graphed habitat variables that appeared in top models ($\Delta\mathrm{QAIC_c} \leq 2.0$) explaining occupancy probability and for which 95% confidence intervals excluded zero.

mounts that many individuals select habitat at multiple scales (Moore and Gillingham 2006, Steen et al. 2010a).

For some species, occupancy modeling confirmed suggestions made elsewhere regarding potentially important habitats. For example, although *C. adamanteus* is thought to primarily select early-successional and/or fire- maintained pine forests and savannas (Waldron et al. 2006, 2008, Hoss et al. 2010), a habitat mosaic is also likely to be important to the species (Hoss et al. 2010), and vegetation structure may be of greater importance than vegetation species composition for *C. adamanteus* (Waldron et al. 2008) and for snakes in general (Reinert 2001). Similarly, *C. adamanteus* used a variety of habitats, including agricultural areas, hardwood, pine, and mixed hardwood–pine forests in southwestern Georgia, although it was not significantly associated with any one of these habitats in particular (Steen et al. 2007b). Because the top model explaining *C. adamanteus* occupancy included five different land cover categories (including evergreen forest; Table 4), our data suggested that habitat heterogeneity at a large spatial scale best predicted whether a site is occupied by *C. adamanteus*. The species was positively and significantly associated with increasing coverage of mixed forest (Fig. 2).

Similar trends were observed for the other rattlesnake species included within this study. *Crotalus horridus* occupancy was also best explained by a model contain-

ing multiple habitat categorizations, but at two scales (250- and 1000-m; Table 4). At both scales, top models indicated a positive but nonsignificant association with deciduous forests (Table 5), which provided partially corroborating evidence that this species uses hardwood forest close to wetlands (Steen et al. 2007b). *Crotalus horridus* was also significantly and negatively associated with scrub/shrub (Fig. 2). Cumulatively, occupancy modeling suggested that large-scale matrices of natural habitats might be important to maintaining rattlesnake populations in the southeastern United States.

Lampropeltis getula is a formerly widespread and common species that has experienced localized and enigmatic declines (Winne et al. 2007, Stapleton et al. 2008). Several models at the 500-m scale garnered strong support (Table 4), suggesting that occupancy for this species was best explained by multiple habitat characteristics. In a separate study in southwestern Georgia (Steen et al. 2010a), *Lampropeltis getula* home ranges were located in pine and hardwood forests more than other habitats, but this apparent preference does not explain declines observed elsewhere (Winne et al. 2007). Occupancy probability for the species decreased with increasing coverage of forest, evergreen forest, and grass (Fig. 2), and a top model revealed a positive but nonsignificant association with deciduous forest and scrub/shrub (Table 5). Our study incorporated both

TABLE 4. Top models explaining variation in occupancy probability for terrestrial snakes of the southern United States.

Species and models	Scale (m)	QAIC$_c$	ΔQAIC$_c$	w_i	$\hat{c}$
Agkistrodon contortrix (430)					
Ψ(Scrub/shrub)	500	1759.39	0.00	0.68	1.06
Ψ(Forest+Allwater)	500	1760.94	1.55	0.32	
Ψ(Scrub/shrub)	1000	1815.91	56.52	0.00	1.02
Ψ(Forest+Allwater)	250	1824.98	65.59	0.00	1.15
Coluber constrictor (449)					
Ψ(Scrub/shrub+Grass)	1000	1933.22	0.00	0.68	1.04
Ψ(Scrub/shrub)	1000	1934.72	1.50	0.32	
Ψ(.)	250	1961.1	27.88	0.00	1.02
Ψ(Scrub/shrub)	500	1996.99	63.77	0.00	1.00
Ψ(Forest)	500	1997.69	64.47	0.00	
Coluber flagellum (431)					
Ψ(Dec+Allwater)	1000	1499.22	0.00	0.69	0.21
Ψ(Forest+Allwater)	1000	1500.87	1.65	0.30	
Ψ(Dec+Allwater)	500	1508.78	9.56	0.01	0.24
Ψ(Forest+Allwater)	250	1514.63	15.41	0.00	0.13
Crotalus adamanteus (123)					
Ψ(Dec+Everg+Mixed+Scrub/Shrub+Grass)	1000	210.92	0.00	1.00	1.28
Ψ(Dec+Everg+Mixed+Scrub/Shrub+Grass)	250	238.59	27.67	0.00	1.42
Ψ(Dec+Allwater)	250	240.03	29.11	0.00	
Ψ(Dec+Everg+Mixed+Scrub/Shrub+Grass)	500	250.39	39.08	0.00	1.20
Crotalus horridus (419)					
Ψ(Dec+Everg+Mixed+Scrub/Shrub+Grass)	1000	349.02	0.00	0.65	0.35
Ψ(Dec+Everg+Mixed+Scrub/Shrub+Grass)	250	350.41	1.39	0.33	0.36
Ψ(Dec+Everg+Mixed+Scrub/Shrub+Grass)	500	355.97	6.95	0.02	0.38
Elaphe guttata (152)					
Ψ(.)	500	308.91	0.00	1.00	1.29
Ψ(Dec+Allwater)	1000	333.59	24.68	0.00	1.18
Ψ(.)	250	393.63	84.72	0.00	1.22
Elaphe obsoleta (449)					
Ψ(Dec+Allwater)	1000	1482.59	0.00	1.00	1.25
Ψ(Dec+Allwater)	500	1632.29	149.70	0.00	1.13
Ψ(Dec+Allwater)	250	1657.94	175.35	0.00	1.12
Elaphe slowinskii (297)					
Ψ(Dec+Everg+Mixed+Scrub/Shrub+Grass)	1000	1164.01	0.00	1.00	1.11
Ψ(Dec+Everg+Mixed+Scrub/Shrub+Grass)	250	1229.87	65.86	0.00	1.05
Ψ(Dec+Everg+Mixed+Scrub/Shrub+Grass)	500	1236.11	72.10	0.00	1.04
Heterodon platirhinos (449)					
Ψ(Roads)	250	471.47	0.00	1.00	3.03
Ψ(Roads)	500	488.9	17.43	0.00	2.92
Ψ(Scrub/shrub)	500	489.27	17.80	0.00	
Ψ(.)	500	490.01	18.54	0.00	
Ψ(Scrub/shrub)	1000	562.28	90.81	0.00	2.51
Lampropeltis getula (449)					
Ψ(Forest+Grass)	500	586.83	0.00	0.33	1.98
Ψ(Everg)	500	587.06	0.23	0.29	
Ψ(Dec+Everg+Mixed+Scrub/Shrub+Grass)	500	587.65	0.82	0.22	
Ψ(.)	500	588.28	1.45	0.16	
Ψ(Forest+Grass)	1000	625.14	38.31	0.00	1.84
Ψ(Everg)	1000	626.53	39.70	0.00	
Ψ(Everg)	250	1053.35	466.52	0.00	1.09
Ψ(.)	250	1053.82	466.99	0.00	
Pituophis melanoleucus (141)					
Ψ(Roads)	250	115.98	0.00	0.27	3.45
Ψ(Forest)	250	116.41	0.43	0.22	
Ψ(Dec)	250	116.69	0.71	0.19	
Ψ(Everg)	250	116.71	0.73	0.19	
Ψ(Scrub/shrub+Grass)	250	117.33	1.35	0.14	
Ψ(Dec+Allwater)	1000	171.64	55.66	0.00	2.19
Ψ(Forest+Allwater)	1000	171.7	55.72	0.00	
Ψ(Roads)	1000	173.37	57.39	0.00	
Ψ(Dec+Everg+Mixed+Scrub/Shrub+Grass)	500	174.79	58.81	0.00	2.07

TABLE 4. Continued.

Species and models	Scale (m)	QAIC$_c$	ΔQAIC$_c$	w_i	$\hat{c}$
Pituophis ruthveni (297)					
Ψ(Dec+Everg+Mixed+Scrub/Shrub+Grass)	1000	340.68	0.00	1.00	0.58
Ψ(Dec+Everg+Mixed+Scrub/Shrub+Grass)	500	354.77	14.09	0.00	0.43
Ψ(Scrub/shrub+Grass)	500	356.25	15.57	0.00	
Ψ(Scrub/shrub)	250	361.16	20.48	0.00	0.37
Ψ(Project)	250	361.18	20.50	0.00	
Ψ(Scrub/shrub+Grass)	250	361.44	20.76	0.00	
Ψ(Dec+Everg+Mixed+Scrub/Shrub+Grass)	250	362.45	21.77	0.00	
Thamnophis sirtalis (449)					
Ψ(.)	250	223.41	0.00	1.00	2.77
Ψ(Scrub/shrub+Grass)	1000	242.84	19.43	0.00	2.50
Ψ(Scrub/shrub+Grass)	500	360.33	136.92	0.00	1.64

Notes: Numbers in parentheses after species are the number of traps included in analysis. Untransformed estimates of coefficients for covariates that appeared in models with ΔQAIC$_c$ ≤ 2.0 appear in Table 5, and relationships between occupancy probabilities and covariates for which 95% confidence intervals did not overlap zero are graphed in Fig. 2.

areas where *L. getula* are captured relatively frequently (e.g., Ichauway; Linehan et al. 2010) and areas where the species is thought to have declined precipitously (e.g., Conecuh National Forest; Guyer et al. 2007). Although many species are of conservation concern due to habitat loss and degradation, this study, together with other recent work (Linehan et al. 2010, Steen et al. 2010*a*), did not identify aspects of *L. getula* spatial ecology or habitat selection that would explain recent enigmatic population declines.

Agkistrodon contortrix may be found in many different habitats across its wide range (Ernst and Ernst 2003). Our data suggest that occupancy is significantly negatively associated with scrub/shrub and significantly positively associated with total forest cover (Fig. 2). A model suggesting a positive but nonsignificant association with wetlands was also important (Table 5).

Heterodon platirhinos is a wide-ranging species for which there are few published studies describing large-scale habitat use in the southern United States. However, individual snakes prefer dry and open habitats in South Carolina (Plummer and Mills 2000) and sandy areas in general (Ernst and Ernst 2003). Occupancy for *H. platirhinos* in this study was best explained by the area of roads at a relatively small spatial scale (Table 4). A potential explanation for this model garnering strong support could be that fragmentation by roads decreases forest canopy cover, benefitting *H. platirhinos*. However, it is unlikely that roads promote population viability (e.g., Plummer and Mills 2006). Alternatively, it is possible that road densities in the southeastern United States are greater on sandy ridges than elsewhere, thus intersecting preferred habitat for *H. platirhinos*.

Although *Elaphe obsoleta* is large and commonly encountered, there have been surprisingly few natural history studies of this species within the southeastern extent of its range. Elsewhere, closely related species are positively associated with forests and edge habitats (Durner and Gates 1993, Keller and Heske 2000, Blouin-Demers and Weatherhead 2001); in the western-

most reach of the southeastern United States, radiotelemetry indicated that *E. obsoleta* were often found in deciduous trees, particularly those with cavities (Pierce et al. 2008). Herein, the model best explaining *E. obsoleta* occupancy contained deciduous forests and aquatic habitats (Tables 4 and 5). Although the species may use wetlands (McAllister 1995), certain forest types associated with aquatic habitats, such as bottomland hardwood forests (Kellison and Young 1997), potentially influenced the trends that we observed.

Pituophis ruthveni is a rarely encountered snake that is difficult to study and is thought to be in decline throughout its limited range (Rudolph et al. 2006); the species is thought to be highly dependent on the frequently burned longleaf pine ecosystem (Himes et al. 2006). Our data suggest that *P. ruthveni* occupancy is significantly and positively associated with evergreen and mixed forests as well as scrub/shrub at a large spatial scale (Fig. 2). Top models also suggested a positive but nonsignificant association with grassland and a negative but also nonsignificant association with deciduous forest (Table 5). *Pituophis ruthveni* is thought to be closely associated with Baird's pocket gopher, *Geomys breviceps*, which is their primary prey (Rudolph et al. 1998, 2002). Although we did not quantify the density of pocket gophers, this may also have an important influence on *P. ruthveni* distribution. *Elaphe slowinskii* is another species within the western extent of our study area for which multiple habitat types at a large scale best predicted occupancy. Occupancy was significantly and positively related to mixed forest as well as grass and scrub/shrub (Fig. 2).

Pituophis melanoleucus is a large species suspected to be in decline across a wide range (Franz 1992). The species was demonstrated to select sandhill and oak hammock habitat in north Florida (Franz 2005), mixed pine–hardwood forests in southwestern Georgia (Miller et al., *in press*), open-field habitats in Tennessee (Gerald et al. 2006), and evergreen forests at a large spatial scale and scrub/shrub habitats at a smaller spatial scale in

TABLE 5. Untransformed estimates of coefficients for covariates appearing in top models ($\Delta QAIC_c \leq 2.0$) explaining occupancy patterns of terrestrial snakes (Table 3) and associated standard errors.

Species, model, and covariate	Beta	SE
Agkistrodon contortrix		
Ψ(Scrub/shrub)		
Scrub/shrub	−0.80	0.21
Ψ(Forest+Allwater)		
Forest	0.91	0.25
Allwater	0.80	0.61
Coluber constrictor		
Ψ(Scrub/shrub+Grass)		
Scrub/shrub	−1.01	0.43
Grass	−0.62	0.30
Ψ(Scrub/shrub)		
Scrub/shrub	−0.83	0.33
Coluber flagellum		
Ψ(Dec+Allwater)		
Dec	9.79	10.95
Allwater	−0.96	0.22
Ψ(Forest+Allwater)		
Forest	−1.39	0.71
Allwater	−1.46	0.45
Crotalus adamanteus		
Ψ(Dec+Everg+Mixed+Scrub/Shrub+Grass)		
Dec	1.78	2.03
Everg	0.40	0.82
Mixed	3.59	1.54
Scrub/shrub	0.60	0.75
Grass	−0.86	0.82
Crotalus horridus		
Ψ(Dec+Everg+Mixed+Scrub/Shrub+Grass)		
Dec	0.80	0.76
Everg	−0.91	0.56
Mixed	−0.34	0.42
Scrub/shrub	−1.40	0.45
Grass	−0.27	0.31
Elaphe obsoleta		
Ψ(Dec+Allwater)		
Dec	4.11	4.91
Allwater	2.02	1.12
Elaphe slowinskii		
Ψ(Dec+Everg+Mixed+Scrub/Shrub+Grass)		
Dec	0.33	0.26
Everg	0.38	0.32
Mixed	1.48	0.51
Scrub/shrub	0.59	0.26
Grass	0.56	0.25
Heterodon platirhinos		
Ψ(Roads)		
Roads	2.06	2.07
Lampropeltis getula		
Ψ(Forest+Grass)		
Forest	−1.95	0.97
Grass	−1.09	0.52
Ψ(Everg)		
Everg	−0.72	0.49
Ψ(Dec+Everg+Mixed+Scrub/Shrub+Grass)		
Dec	6.57	7.20
Everg	−2.43	1.04
Mixed	−1.10	0.56
Scrub/shrub	0.61	1.26
Grass	−1.34	0.56

TABLE 5. Continued.

Species, model, and covariate	Beta	SE
Pituophis melanolecus		
Ψ(Roads)		
Roads	−7.11	11.84
Ψ(Forest)		
Forest	1.01	0.89
Ψ(Dec)		
Dec	2.50	11.13
Ψ(Everg)		
Everg	1.11	2.6
Ψ(Scrub/shrub+Grass)		
Scrub/shrub	9.84	10.46
Grass	−1.31	1.34
Pituophis ruthveni		
Ψ(Dec+Everg+Mixed+Scrub/Shrub+Grass)		
Dec	−2.36	2.39
Everg	2.65	1.12
Mixed	0.80	0.40
Scrub/shrub	2.46	0.83
Grass	0.16	0.60

Mississippi (Baxley et al. 2011). Cumulatively, these studies indicate that individuals may use open-canopy habitats within forests of any type. We did not identify significant associations between occupancy and any land cover type for this species, but several habitat features (i.e., forests of multiple types and scrub/shrub) appeared in top models for *P. melanoleucus* at a relatively small spatial scale (Tables 4 and 5). Some of these habitat types are the same as those identified as important elsewhere (e.g., Gerald et al. 2006, Baxley et al. 2011, Miller et al., *in press*). A negative but nonsignificant relationship with roads was also suggested by a top model (Table 5); radiotelemetered individuals in southwestern Georgia crossed paved and graded roads less frequently than would be expected by chance (Miller et al., *in press*), and snakes in the genus may be vulnerable to road mortality (e.g., Rudolph and Burgdorf 1997, Rudolph et al. 1999) due to their large size, extensive movements, and relatively slow speed. In summary, top models for *P. melanoleucus* suggest that occupancy was best explained by several forest and open-canopy habitats; fragmentation by roads may be an impediment to maintaining viable populations.

Both *Coluber* species included within this study are active foragers that are sympatric throughout the southeastern United States, with some degree of resource partitioning (Halstead et al. 2008). At a large spatial scale, occupancy probabilities of the two species were influenced by different landscape-level habitat features. *Coluber constrictor* occupancy was significantly and negatively related to scrub/shrub and grassland habitats (Table 5, Fig. 2), suggesting that the species is less likely to be found in open landscapes similar to those identified elsewhere as important for *C. flagellum* (Halstead et al. 2009). Conversely, *C. flagellum* occupancy was best explained by models indicating a positive but nonsignificant association with deciduous forests

and a negative but nonsignificant association with forests in general; the species was significantly and negatively associated with aquatic habitats (Table 5, Fig. 2). These results are generally consistent with the species' tendency to prefer dry, upland areas (Ernst and Ernst 2003, Halstead et al. 2009) and oak savannas over pine (Johnson et al. 2007).

For two species, we were unable to identify habitat features that were important influences of occupancy. Top models for both *E. guttata* and *Thamnophis sirtalis* suggested that occupancy was constant across all sites (Table 4). *T. sirtalis* is one of the most widespread species within North America, found in diverse habitats from peninsular Florida north to Hudson Bay, Canada, and west to California (Ernst and Ernst 2003). Our inability to identify important habitat features may be a consequence of the generalist habitat use of this species. However, *T. sirtalis* is often considered to be associated with wetland habitats (Ernst and Ernst 2003). Our failure to identify wetlands as an important covariate may be an artifact of our methodology, which related occupancy to extent of a particular land cover type. Further occupancy modeling, including wetland presence as a categorical variable, may reveal whether *T. sirtalis* is positively associated with this habitat type. However, *T. sirtalis* may benefit from wetlands small enough that they are excluded from the 30-m resolution of the National Land Cover Data.

Elaphe guttata is also known to use a variety of terrestrial habitats (Franz 1995, Ernst and Ernst 2003), but is restricted primarily to the southeastern United States, with relict populations in Kentucky and New Jersey. It is possible that *E. guttata* occupancy is influenced by a habitat (or a spatial scale) that we did not include in this study. Alternatively, the distribution of *E. guttata* may be largely a consequence of physiological limitations, rather than landscape features, with the species occurring in any suitable terrestrial habitat within in its range. For example, as ectotherms, snakes may be particularly sensitive to variation in thermal quality (Row and Blouin-Demers 2006). *Elaphe guttata* may be ill-equipped to persist in areas where temperatures are relatively low.

Crotalus adamanteus and *P. ruthveni* are both highly associated with longleaf pine forests (Guyer and Bailey 1993, Means 2006, Rudolph et al. 2006), an imperiled habitat often degraded due to fire suppression and subsequent increases in hardwood tree density (Mitchell et al. 2006). Degraded longleaf pine forests are typically restored by removal of hardwood trees, and land managers maintain low hardwood and woody vegetation densities through the use of hardwood reduction techniques, particularly prescribed fire (Brockway et al. 2005). These efforts may be undertaken specifically to improve habitat suitability for imperiled wildlife (USFWS 2003*a*, *b*) Target hardwood densities may vary, but are generally very low (Provencher et al. 2001, Kush et al. 2004), despite hardwood trees being

historical components of longleaf pine forests (Frost 1993). However, hardwood trees may provide resources, such as refugia and food, for many species, including those considered longleaf pine specialists (Perkins et al. 2008). We documented significant, positive relationships between *C. adamanteus* and *P. ruthveni* occupancy and mixed forests (Fig. 2), suggesting that although frequently burned longleaf pine forests may be the primary habitat association of these species, habitat suitability is influenced heavily by the presence of at least some hardwood trees within these forests.

The data included in this analysis were typically associated with studies or monitoring programs in relatively large and undeveloped areas. Therefore, we suggest that our results are probably most appropriate in identifying habitats important for snakes in natural settings with limited human disturbance. These findings may be most appropriate when designing restoration goals or identifying potential reintroduction sites. However, we acknowledge that sites may possess diverse land-use histories, which may include impacts from past fire suppression, roads, silviculture, or agricultural activity, among other anthropogenic disturbances, and disparate land-use histories may influence current occupancy patterns of wildlife (Piha et al. 2007). Thus, our inferential power would be stronger if all sites were components of a single experimental design and subject to controlled study. Such are the trade-offs of large-scale collaborative efforts.

The occupancy of any given species may be influenced by variables that were not measured in our study, including the presence or abundance of prey, microhabitat features such as belowground refugia, or percent canopy cover, among other potentials. How a particular habitat is managed may also influence habitat suitability (Russell et al. 2004), and snake abundances may be altered following different management strategies (Todd and Andrews 2008). However, given that the species included within this study are not generally considered habitat specialists, it is unlikely that a species would become extirpated following habitat management, provided there was not conversion to an alternate, unsuitable habitat (e.g., evergreen to deciduous forest, or forest to agriculture; Driscoll 2004). This degree of response (i.e., extirpation) may be required to influence the findings presented herein, given that our analysis incorporated variation in detection probability and relatively broad land cover categories (Table 2). In addition, we did not identify project as an important covariate for any species, suggesting that there were no site-specific features that were important influences of occupancy yet not measured within this study.

Habitat patch size may also be an important consideration influencing occupancy (Luiselli and Capizzi 1997, Kjoss and Litvaitis 2001; but see Prugh et al. 2008). However, given that we have a poor understanding of edge permeability related to snake metapopulation dynamics, any attempt to infer ecological

significance from habitat type or study area boundaries would be subjective. Although identifying suitable patch size was outside the scope of this study, the large size of most forests within this study suggests that they are unlikely to be below minimum area thresholds necessary to sustain a species in a given area. Because traps were located in natural areas with limited anthropogenic development, it is unlikely that we would have identified roads as an important covariate; occupancy studies conducted over a more diverse landscape are more likely to identify thresholds of anthropogenic development influencing the occupancy of snake species (e.g., Baxley et al. 2011).

Species-level occupancy modeling, which incorporates variation in detection probability, may identify habitat features important for vertebrate population persistence at large spatial scales (e.g., Karanth et al. 2009). In addition, these analyses may indicate that vertebrates select habitat on the species level in a manner different than would be expected based on use of intrinsic habitat features on small spatial scales (e.g., Ruiz-Gutiérrez et al. 2010). Our analysis identified that landscape-level features may be important influences in terrestrial snake occupancy. Therefore, if future studies aim to identify habitat features important for snakes, they should differentiate between the landscape features that affect whether a snake species occurs at a given site and the habitats used by individual snakes at that site. Many terrestrial snakes in the southeastern United States are of conservation concern (e.g., USFWS 1982, Martin and Means 2000, Tuberville et al. 2000, Krysko and Smith 2005). As interest increases in the conservation of this imperiled group, studies like ours, identifying habitat associations at multiple scales, may be important when generating management plans.

Literature Cited

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Baxley, D., G. J. Lipps, Jr., and C. P. Qualls. 2011. Multiscale habitat selection by black pine snakes (*Pituophis melanoleucus lodingi*) in southern Mississippi. Herpetologica 67:154–166.

Baxley, D., and C. Qualls. 2009. Habitat associations of reptile and amphibian communities in longleaf pine habitats of south Mississippi. Herpetological Conservation and Biology 3:295–305.

Blouin-Demers, G., and P. J. Weatherhead. 2001. Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. Ecology 82:2882–2896.

Brockway, D. G., K. W. Outcalt, D. J. Tomczak, and E. E. Johnson. 2005. Restoration of longleaf pine ecosystems. USDA Forest Service General Technical Report SRS-83. USDA Forest Service, Southern Research Station, Asheville, North Carolina, USA.

Buler, J. J., F. R. Moore, and S. Woltmann. 2007. A multi-scale examination of stopover habitat use by birds. Ecology 88:1789–1802.

Burbrink, F. T. 2001. Systematics of the eastern ratsnake complex (*Elaphe obsoleta*). Herpetological Monographs 15:1–53.

Burbrink, F. T. 2002. Phylogeographic analysis of the corn-snake (*Elaphe guttata*) complex as inferred from maximum likelihood and Bayesian analyses. Molecular Phylogenetics and Evolution 25:465–476.

Burbrink, F. T., R. Lawson, and J. B. Slowinski. 2000. Mitochondrial DNA phylogeography of the polytypic North American rat snake (*Elaphe obsoleta*): a critique of the subspecies concept. Evolution 54:2107–2118.

Burgdorf, S. J., D. C. Rudolph, R. N. Conner, D. Saenz, and R. R. Schaefer. 2005. A successful trap design for capturing large terrestrial snakes. Herpetological Review 36:421–424.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference. Second edition. Springer-Verlag, New York, New York, USA.

Cagle, N. L. 2008. Snake species distributions and temperate grasslands: a case study from the American tallgrass prairie. Biological Conservation 141:744–755.

Conner, L. M., and B. W. Plowman. 2001. Using Euclidean distances to assess nonrandom habitat use. Pages 275–290 *in* J. Millspaugh and J. Marzluff, editors. Radio telemetry and animal populations. Academic Press, San Diego, California, USA.

Dodd, C. K., Jr. 1987. Status, conservation, and management. Pages 478–513 *in* R. A. Seigel, J. T. Collins, and S. S. Novak, editors. Snakes: ecology and evolutionary biology. MacMillan, New York, New York, USA.

Driscoll, D. 2004. Extinction and outbreaks accompany fragmentation of a reptile community. Ecological Applications 14:220–240.

Durner, G. M., and J. E. Gates. 1993. Spatial ecology of black rat snakes on Remington Farms, Maryland. Journal of Wildlife Management 57:812–826.

Durso, A. M., J. D. Willson, and C. T. Winne. 2011. Needles in haystacks: estimating detection probability and occupancy of rare and cryptic snakes. Biological Conservation 144:1508–1515.

Ernst, C. H., and E. M. Ernst. 2003. Snakes of the United States and Canada. Smithsonian Institution Press, Washington, D.C., USA.

ESRI. 2009. ArcGIS version 9.3.1. Environmental Systems Research Institute, Redlands, California, USA.

Ford, N. B., V. A. Cobb, and J. Stout. 1991. Species diversity and seasonal abundance of snakes in a mixed pine–hardwood forest of eastern Texas. Southwestern Naturalist 36:171–177.

Franz, R. 1992. Florida pine snake, *Pituophis melanoleucus mugitus* Barbour. Pages 254–258 *in* P. E. Moler, editor. Rare

and endangered biota of Florida. Volume 3. Amphibians and reptiles. University Press of Florida, Gainesville, Florida, USA.

Franz, R. 1995. Habitat use, movements and home range in two species of ratsnakes (genus *Elaphe*) in a north Florida sandhill. Florida Game and Fresh Water Fish Commission Nongame Wildlife Program Project Report, Tallahassee, Florida, USA.

Franz, R. 2005. Up close and personal: a glimpse into the life of the Florida pine snake in a north Florida sandhill. Pages 120–131 *in* W. E. Meshaka, Jr., and K. J. Babbitt, editors. Amphibians and reptiles: status and conservation in Florida. Krieger Publishing Company, Malabar, Florida, USA.

Frost, C. C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Pages 17–43 *in* S. M. Hermann, editor. Proceedings of the Tall Timbers Fire Ecology Conference Number 18. The Longleaf Pine Ecosystem: ecology, restoration and management. Tall Timbers Research Station, Tallahassee, Florida, USA.

Gardner, T. A., J. Barlow, and C. A. Peres. 2007. Paradox, presumption and pitfalls in conservation biology: the importance of habitat change for amphibians and reptiles. Biological Conservation 138:166–179.

Gerald, G. W., M. A. Bailey, and J. N. Holmes. 2006. Habitat utilization of *Pituophis melanoleucus melanoleucus* (northern pinesnakes) on Arnold Air Force Base in middle Tennessee. Southeastern Naturalist 5:253–264.

Gibbons, J. W., D. E. Scott, T. J. Ryan, K. A. Buhlmann, T. D. Tuberville, B. S. Metts, J. L. Greene, T. Mills, Y. Leiden, S. Poppy, and C. T. Winne. 2000. The global decline of reptiles, déjà vu amphibians. BioScience 50:653–666.

Greene, H. W. 2005. Organisms in nature as a central focus for biology. Trends in Ecology and Evolution 20:23–27.

Guyer, C., and M. A. Bailey. 1993. Amphibians and reptiles of longleaf pine communities. Pages 139–158 *in* S. M. Hermann, editor. Proceedings of the Tall Timbers Fire Ecology Conference Number 18. The Longleaf Pine Ecosystem: ecology, restoration and management. Tall Timbers Research Station, Tallahassee, Florida, USA.

Guyer, C., M. A. Bailey, J. N. Holmes, J. A. Stiles, and S. H. Stiles. 2007. Herpetofaunal response to longleaf pine ecosystem restoration, Conecuh National Forest, Alabama. Final report to the Alabama Department of Conservation and Natural Resources and the U.S. Forest Service. http://www.dcnr.state.al.us/research-mgmt/State%20Wildlife%20Grants/Conecuh_NF_Final_Herp_Report_April_2007.pdf

Halstead, B. J., H. R. Mushinsky, and E. D. McCoy. 2008. Sympatric *Masticophis flagellum* and *Coluber constrictor* select vertebrate prey at different levels of taxonomy. Copeia 2008:897–908.

Halstead, B. J., H. R. Mushinsky, and E. D. McCoy. 2009. *Masticophis flagellum* selects Florida scrub habitat at multiple scales. Herpetologica 65:268–279.

Himes, J. G., L. M. Hardy, D. C. Rudolph, and S. J. Burgdorf. 2006. Movement patterns and habitat selection by native and repatriated Louisiana pine snakes (*Pituophis ruthveni*): implications for conservation. Herpetological Natural History 9:103–116.

Hines, J. E. 2010. PRESENCE3-Software to estimate patch occupancy and related parameters. USGS-PWRC, Patuxent Wildlife Research Center, Laurel, Maryland, USA. http://www.mbr-pwrc.usgs.gov/software/presence.html

Homer, C., C. Huang, L. Yang, B. Wylie, and M. Coan. 2004. Development of a 2001 National Land Cover Database for the United States. Photogrammetric Engineering and Remote Sensing 70:829–840.

Hoss, S. K., C. Guyer, L. L. Smith, and G. W. Schuett. 2010. Multiscale influences of landscape composition and configuration on the spatial ecology of eastern diamond-backed rattlesnakes (*Crotalus adamanteus*). Journal of Herpetology 44:110–123.

Humphries, W. J. 2005. Relationships between amphibian and reptile communities and forest management in upland pine stands of the South Carolina coastal plain. Dissertation. Clemson University, Clemson, South Carolina.

Jenkins, C. L., C. R. Peterson, and B. A. Kingsbury. 2009. Modeling snake distribution and habitat. Pages 123–148 *in* S. J. Mullin and R. A. Seigel, editors. Snakes: ecology and conservation. Cornell University Press, Ithaca, New York, USA.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johnson, R. W., R. R. Fleet, M. B. Keck, and D. C. Rudolph. 2007. Spatial ecology of the coachwhip, *Masticophis flagellum* (Squamata: Colubridae), in eastern Texas. Southeastern Naturalist 6:111–124.

Karanth, K. K., J. D. Nichols, J. E. Hines, K. U. Karanth, and N. L. Christensen. 2009. Patterns and determinants of mammal species occurrence in India. Journal of Applied Ecology 46:1189–1200.

Keller, W. L., and E. J. Heske. 2000. Habitat use by three species of snakes at the Middle Fork Fish and Wildlife Area, Illinois. Journal of Herpetology 34:558–564.

Kellison, R. C., and M. J. Young. 1997. The bottomland hardwood forest of the southern United States. Forest Ecology and Management 90:101–115.

Kéry, M. 2002. Inferring the absence of a species: a case study of snakes. Journal of Wildlife Management 66:330–338.

Kjoss, V. A., and J. A. Litvaitis. 2001. Community structure of snakes in a human-dominated landscape. Biological Conservation 98:285–292.

Koons, D. N., R. D. Birkhead, S. M. Boback, M. I. Williams, and M. P. Greene. 2009. The effect of body size on cottonmouth (*Agkistrodon piscivorus*) survival, recapture probability, and behavior in an Alabama swamp. Herpetological Conservation and Biology 4:221–235.

Krysko, K. L., and D. J. Smith. 2005. The decline and extirpation of the kingsnake (*Lampropeltis getula*) in Florida. Pages 132–141 *in* W. E. Meshaka, Jr., and K. J. Babbitt, editors. Amphibians and reptiles: status and conservation in Florida. Krieger Publishing, Malabar, Florida, USA.

Kush, J. S., R. S. Meldahl, and C. Avery. 2004. A restoration success: longleaf pine seedlings established in a fire-suppressed, old-growth stand. Ecological Restoration 22:6–10.

Lagory, K. E., L. J. Walston, C. Goulet, R. A. Van Lonkhuyzen, S. Najjar, and C. Andrews. 2009. An examination of scale-dependent resource use by eastern hognose snakes in south-central New Hampshire. Journal of Wildlife Management 73:1387–1393.

Lee, J. R. 2009. The herpetofauna of the Camp Shelby Joint Forces Training Center in the Gulf Coastal Plain of Mississippi. Southeastern Naturalist 8:639–652.

Lind, A. J., H. H. Welsh, Jr., and D. A. Tallmon. 2005. Garter snake population dynamics from a 16-year study: considerations for ecological monitoring. Ecological Applications 15:294–303.

Linehan, J. M., L. L. Smith, and D. A. Steen. 2010. Ecology of the eastern kingsnake (*Lampropeltis getula getula*) in a longleaf pine (*Pinus palustris*) forest in southwestern Georgia. Herpetological Conservation and Biology 5:94–101.

Long, R. A., T. M. Donovan, P. MacKay, W. J. Zielinski, and J. S. Buzas. 2011. Predicting carnivore occurrence with noninvasive surveys and occupancy modeling. Landscape Ecology 26:327–340.

Luiselli, L. 2006. Site occupancy and density of sympatric Gaboon viper (*Bitis gabonica*) and nose-horned viper (*Bitis nasicornis*). Journal of Tropical Ecology 22:555–564.

Luiselli, L., and D. Capizzi. 1997. Influences of area, isolation and habitat features on distribution of snakes in Mediterra-

nean fragmented woodlands. Biodiversity and Conservation 6:1139–1351.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

Martin, W. H., and D. B. Means. 2000. Geographic distribution and habitat relationships of the eastern diamondback rattlesnake, Crotalus adamanteus. Herpetological Natural History 7:9–35.

Mazerolle, M. J., L. L. Bailey, W. L. Kendall, J. A. Royle, S. J. Converse, and J. D. Nichols. 2007. Making great leaps forward: accounting for detectability in herpetological field studies. Journal of Herpetology 41:672–689.

Mazerolle, M. J., A. Desrochers, and L. Rochefort. 2005. Landscape characteristics influence pond occupancy by frogs after accounting for detectability. Ecological Applications 15:824–834.

McAllister, A. J. 1995. Wetland habitat use by the black rat snake, Elaphe obsoleta, in eastern Ontario. Canadian Field-Naturalist 109:449–451.

Means, D. B. 2006. Vertebrate faunal diversity of longleaf pine ecosystems. Pages 157–213 in S. Jose, E. J. Jokela, and D. L. Miller, editors. The longleaf pine ecosystem: ecology, silviculture, and restoration. Springer, New York, New York, USA.

Means, D. B., and D. Simberloff. 1987. The peninsula effect: habitat-correlated species decline in Florida's herpetofauna. Journal of Biogeography 14:551–568.

Miller, G. J., L. L. Smith, S. A. Johnson, and R. Franz. In press. Home range size and habitat selection in the Florida pine snake (Pituophis melanoleucus mugitus). Copeia.

Mitchell, R. J., J. K. Hiers, J. J. O'Brien, S. B. Jack, and R. T. Engstrom. 2006. Silviculture that sustains: the nexus between silviculture, frequent prescribed fire, and conservation of biodiversity in longleaf pine forests of the southeastern United States. Canadian Journal of Forest Research 36:2723–2736.

Moore, J. A., and J. C. Gillingham. 2006. Spatial ecology and multi-scale habitat selection by a threatened rattlesnake: the eastern massasauga (Sistrurus catenatus catenatus). Copeia 2006:742–751.

Mullin, S. J., and R. A. Seigel. 2009. Snakes: ecology and conservation. Cornell University Press, Ithaca, New York, USA.

Perkins, M. W., L. M. Conner, and M. B. Howze. 2008. The importance of hardwood trees in the longleaf pine forest ecosystem for Sherman's fox squirrels. Forest Ecology and Management 255:1618–1625.

Pierce, J. B., R. R. Fleet, L. McBrayer, and D. C. Rudolph. 2008. Use of trees by the Texas ratsnake (Elaphe obsoleta) in eastern Texas. Southeastern Naturalist 7:359–366.

Piha, H., M. Luoto, and J. Merilä. 2007. Amphibian occurrence is influenced by current and historic landscape characteristics. Ecological Applications 17:2298–2309.

Plummer, M. V., and N. E. Mills. 2000. Spatial ecology and survivorship of resident and translocated hognose snakes (Heterodon platirhinos). Journal of Herpetology 34:565–575.

Plummer, M. V., and N. E. Mills. 2006. Heterodon platirhinos (Eastern hognose snake). Road crossing behavior. Herpetological Review 37:352.

Provencher, L., B. J. Herring, D. R. Gordon, H. L. Rodgers, G. W. Tanner, J. L. Hardesty, L. A. Brennan, and A. R. Litt. 2001. Longleaf pine and oak responses to hardwood reduction techniques in fire-suppressed sandhills in northwest Florida. Forest Ecology and Management 148:63–77.

Prugh, L. R., K. E. Hodges, A. R. E. Sinclair, and J. S. Brashares. 2008. Effect of habitat area and isolation on fragmented animal populations. Proceedings of the National Academy of Sciences USA 105:20770–20775.

Pyron, R. A., and F. T. Burbrink. 2009a. Lineage diversification in a widespread species: roles for niche divergence and conservatism in the common kingsnake, Lampropeltis getula. Molecular Ecology 18:3443–3457.

Pyron, R. A., and F. T. Burbrink. 2009b. Systematics of the common kingsnake (Lampropeltis getula; Serpentes: Colubridae) and the burden of heritage in taxonomy. Zootaxa 2241:22–32.

Reading, C. J., L. M. Luiselli, G. C. Akani, X. Bonnet, G. Amori, J. M. Ballouard, E. Filippi, G. Naulleau, D. Pearson, and L. Rugiero. 2010. Are snake populations in widespread decline? Biology Letters 23:777–780.

Reichling, S. B. 1995. The taxonomic status of the Louisiana pine snake (Pituophis melanoleucus ruthveni) and its relevance to the evolutionary species concept. Journal of Herpetology 29:186–198.

Reinert, H. K. 2001. Habitat selection in snakes. Pages 201–240 in R. A. Seigel and J. T. Collins, editors. Snakes: ecology and behavior. Blackburn Press, Caldwell, New Jersey, USA.

Rodríguez-Robles, J. A., and J. M. De Jesús-Escobar. 2000. Molecular systematics of new world gopher, bull, and pinesnakes (Pituophis: Colubridae), a transcontinental species complex. Molecular Phylogenetics and Evolution 14:35–50.

Roe, J. H., B. A. Kingsbury, and N. R. Herbert. 2003. Wetland and upland use patterns in semi-aquatic snakes: implications for wetland conservation. Wetlands 23:1003–1014.

Row, J. R., and G. Blouin-Demers. 2006. Thermal quality influences effectiveness of thermal regulation, habitat use, and behaviour in milk snakes. Oecologia 148:1–11.

Rudolph, D. C., and S. J. Burgdorf. 1997. Timber rattlesnakes and Louisiana pine snakes of the west Gulf Coastal Plain: hypotheses of decline. Texas Journal of Science 49:111–122.

Rudolph, D. C., S. J. Burgdorf, R. N. Conner, C. S. Collins, D. Saenz, R. R. Schaefer, and T. Trees. 2002. Prey handling and diet of Louisiana pine snakes (Pituophis ruthveni) and black pine snakes (P. melanoleucus lodingi), with comparisons to other selected colubrid snakes. Herpetological Natural History 9:57–62.

Rudolph, D. C., S. Burgdorf, R. Conner, and R. Schaefer. 1999. Preliminary evaluation of the impact of roads and associated vehicular traffic on snake populations in eastern Texas. Pages 129–136 in G. L. Evink, P. Garrett, and D. Zeigler, editors. Proceedings of the Third International Conference on Wildlife Ecology and Transportation. FL-ER-73-99, Florida Department of Transportation, Tallahassee, Florida, USA.

Rudolph, D. C., S. J. Burgdorf, R. R. Schaefer, R. N. Conner, and R. W. Maxey. 2006. Status of Pituophis ruthveni (Louisiana pine snake). Southeastern Naturalist 5:463–472.

Rudolph, D. C., S. J. Burgdorf, J. C. Tull, M. Ealy, R. N. Conner, R. R. Schaefer, and R. R. Fleet. 1998. Avoidance of fire by Louisiana pine snakes, Pituophis melanoleucus ruthveni. Herpetological Review 29:146–148.

Ruiz-Gutiérrez, V., E. F. Zipkin, and A. A. Dhondt. 2010. Occupancy dynamics in a tropical bird community: unexpectedly high forest use by birds classified as non-forest species. Journal of Applied Ecology 47:621–630.

Russell, K. R., T. B. Wigley, W. M. Baughman, H. G. Hanlin, and W. M. Ford. 2004. Response of southeastern amphibians and reptiles to forest management: a review. Pages 319–334 in H. M. Rauscher and K. Johnsen, editors. Southern forest science: past, present, and future. Southern Research Station, Asheville, North Carolina, USA.

Stapleton, S. P., K. J. Sash, D. B. Means, W. E. Palmer, and J. P. Carroll. 2008. Eastern kingsnake (Lampropeltis g. getula) population decline in northern Florida and southern Georgia. Herpetological Review 39:33–35.

Steen, D. A. 2010. Snakes in the grass: secretive natural histories defy both conventional and progressive statistics. Herpetological Conservation and Biology 5:183–188.

Steen, D. A., C. Guyer, and L. L. Smith. 2012. A case study of relative abundance in snakes. Pages 287–294 in R. W. McDiarmid, M. S. Foster, C. Guyer, J. W. Gibbons, and N. Chernoff, editors. Reptile biodiversity: standard methods for inventory and monitoring. University of California Press, Berkeley, California, USA.

Steen, D. A., J. M. Linehan, and L. L. Smith. 2010a. Multiscale habitat selection and refuge use of common kingsnakes, Lampropeltis getula, in southwestern Georgia. Copeia 2010:227–231.

Steen, D. A., G. J. Miller, S. C. Sterrett, and L. L. Smith. 2007a. Masticophis flagellum (eastern coachwhip). Growth and movement. Herpetological Review 38:90.

Steen, D. A., A. E. Rall-McGee, S. M. Hermann, J. A. Stiles, S. H. Stiles, and C. Guyer. 2010b. Effects of forest management on amphibians and reptiles: generalist species obscure trends among native forest associates. Open Environmental Sciences 4:24–30.

Steen, D. A., L. L. Smith, L. M. Conner, J. C. Brock, and S. K. Hoss. 2007b. Habitat use of sympatric rattlesnake species within the Gulf Coastal Plain. Journal of Wildlife Management 71:759–764.

Stevenson, D. J., K. J. Dyer, and B. A. Willis-Stevenson. 2003. Survey and monitoring of the eastern indigo snake in Georgia. Southeastern Naturalist 2:393–408.

Sutton, W. B., Y. Wang, and C. J. Schweitzer. 2010. Habitat relationships of reptiles in pine beetle disturbed forests of Alabama, U.S.A. with guidelines for a modified drift-fence sampling method. Current Zoology 56:411–420.

Todd, B. D., and K. A. Andrews. 2008. Response of a reptile guild to forest harvesting. Conservation Biology 22:753–761.

Todd, B. D., and B. B. Rothermel. 2006. Assessing quality of clearcut habitats for amphibians: effects on abundances versus vital rates in the southern toad (Bufo terrestris). Biological Conservation 133:178–185.

Tuberville, T. D., J. R. Bodie, J. B. Jensen, L. V. LaClaire, and J. W. Gibbons. 2000. Apparent decline of the southern hognose snake (Heterodon simus). Journal of the Elisha Mitchell Scientific Society 116:19–40.

USFWS (U.S. Fish and Wildlife Service). 1982. Eastern indigo snake recovery plan. U.S. Fish and Wildlife Service, Atlanta, Georgia, USA.

USFWS (U.S. Fish and Wildlife Service). 2003a. Recovery plan for the Red-cockaded Woodpecker (Picoides borealis): second revision. U.S. Fish and Wildlife Service, Atlanta, Georgia, USA.

USFWS (U.S. Fish and Wildlife Service). 2003b. Candidate conservation agreement for the Louisiana pine snake, Pituophis ruthveni. U.S. Fish and Wildlife Service, Lufkin, Texas, USA.

Vitt, L. A. 2001. Communities. Pages 335–365 in: R. A. Seigel, J. T. Collins, and S. S. Novak, editors. Snakes: ecology and evolutionary biology. Blackburn Press, Caldwell, New Jersey, USA.

Waldron, J. L., S. H. Bennett, S. M. Welsch, M. E. Dorcas, J. D. Lanham, and W. Kalinowsky. 2006. Habitat specificity and home-range size as attributes of species vulnerability to extinction: a case study using sympatric rattlesnakes. Animal Conservation 9:414–420.

Waldron, J. L., S. M. Welch, and S. H. Bennett. 2008. Vegetation structure and the habitat specificity of a declining North American reptile: a remnant of former landscapes. Biological Conservation 141:2477–2482.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. BioScience 48:607–615.

Willson, J. D., C. T. Winne, and B. D. Todd. 2011. Ecological and methodological factors affecting detectability and population estimation in elusive species. Journal of Wildlife Management 75:36–45.

Winne, C. T., J. D. Willson, B. D. Todd, K. M. Andrews, and J. W. Gibbons. 2007. Enigmatic decline of a protected population of eastern kingsnakes, Lampropeltis getula, in South Carolina. Copeia 2007:507–519.